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REVIEW ARTICLE

Bark beetles in the Tatra Mountains. International research 1998–2005 – an overview

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Abstract

This paper is a review of fundamental information on bark beetles and their interactions with several predisposing factors (air pollution, drought/temperature interactions, windthrows, management activities) that are thought to contribute to the outbreaks in the High Tatra Mountains.

The findings of many research projects indicate that the impact of air pollution on bark beetle populations is indirect and complex and that the disturbances in the physiology and natural resistance of trees may be of crucial importance to bark beetle population dynamics. An active forest protection approach is needed to be applied to the secondary Norway spruce forests affected in the past by human activity.

Bark beetle populations in natural and near-natural forests (mainly in the upper montane zone) are regulated by natural mechanisms; bark beetles are therefore a natural factor contributing to forest development, including the transition of future generations of spruce.

Key words

bark beetles, driving factors, *Picea abies*, population dynamics, Tatra Mountains, Poland, Slovakia

Introduction

The Tatra Mountains are the highest mountain range in the Carpathian Arch forming a natural border between Slovakia and Poland. 75% of their area is located in Slovakia and 25% in Poland. The Tatra Mountains are also one of the most protected areas in the Carpathians with two National Parks: the Tatra National Park in Slovakia (TANAP) created in 1949 with an area of 113,221 hectares and the Tatra National Park (TPN) in Poland created in 1954 with an area of 21,164 hectares. In 1993, the Polish and Slovakian National Parks were jointly designated a transboundary biosphere reserve by UNESCO under its Man and Biosphere Reserve Programme (Mirek 1996).

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The Norway spruce *Picea abies* (L.) Karst. is one of the most important tree species in the High Tatra Mountains which occurs naturally in the upper montane zone. It is also present in the lower montane zone mainly as a result of intensive silvicultural management practiced at the turn of the 19th century.

The spruce bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) is known as a serious pest of spruce monocultures in Eurasia (Christiansen and Bakke 1988, Turčáni and Novotný 1998, Skuhravy 2002). In normally functioning and balanced ecosystems, *I. typographus* is not considered to be an aggressive or primary mortality-causing agent of healthy trees. However, under favourable conditions it is likely to attack healthy trees and regarded as the major direct cause of tree mortality (Christiansen and Huse 1980, Christiansen 1989). This refers especially to spruce stands damaged by wind (Capecki 1978, 1981, Göthlin et al. 2000, Lindelöw and Schroeder 2001), snow (Schroeder and Eidmann 1993), drought (Christiansen and Bakke 1996, Grodzki 1998b) or air pollution (Baltensweiler 1985, Christiansen 1989, Grodzki et al. 2004). The wind thrown trees where bark beetles reproduce must be removed prior to the emergence of the first generation of adults.

Ips typographus is most injurious first of all to mature spruce stands established by planting. *Pityogenes chalcographus* (L.) attacks young (10–20 year old) and middle aged (20–40 year old) spruce stands, but under certain conditions it can also attack older stands (Grodzki 1997b). *Ips amitinus* Eichh. is associated with *I. typographus* at higher altitudes, whereas *Polygraphus polygraphus* (L.) is a species which occurs in older spruce stands affected by air pollution and frequently attacked by root fungal diseases, *i.e. Armillaria* spp. (Kisielowski 1978, Turčáni et al. 2006).

Massive bark beetle outbreaks associated with prior water shortages have been observed several times in the Carpathians (Grodzki 1998a, 2010), and recently also in the Tatra Mountains (Grodzki et al. 2003, 2006a). Also the role of air pollution in the population dynamics of bark beetles has recently been evaluated (Turčáni et al. 2003, Grodzki et al. 2004).

As suggested above, the spatio-temporal pattern of bark beetle population fluctuations depends on many factors. Spatial synchrony between populations of the same species has been documented for a variety of taxa. One of the characteristics of spatially synchronous population dynamics is that nearby populations tend to be more synchronous than those separated by long distances. Basing on this pattern, two hypotheses of the causes of spatial synchrony have been formulated: 1) that synchronization is via the migration of members (or predators) between populations or 2) that synchronization of populations is via the spatially synchronous stochastic effects (i.e. weather) (Raimondo et al. 2004). Bark beetle populations seem to be less synchronous than defoliator populations (Økland et al. 2005). This might be attributed to local stochastic effects (powerful winds, snow) operating on relatively small areas and resulting in a smaller spatial autocorrelation between populations. The temporal pattern of fluctuations indicates the existence of some regular cycling, so the suggestion that it is controlled by stochastic factors, such as weather is difficult to verify (Turčáni – unpublished data). Both patterns need to be analysed more precisely to understand the mechanisms of bark beetles outbreaks.

The paper focuses on the fundamental information about bark beetles and their interactions with several predisposing factors that are thought to contribute to the outbreaks of this pest species in the High Tatra Mountains. These include air pollution, drought/temperature interactions, windthrows, and management activities. Since the bark beetle populations are extremely important in the ecosystems of the High Tatra spruce forests, it is necessary to understand the processes that influence their population dynamics, as well as the dynamics of natural spruce forests in this region and in the entire Carpathian range.

Bark beetles and air pollution stress in the Tatra Mountains

Attempts have been made to better understand the possible impact of air pollution, especially the ozone level on the populations of bark beetles, mainly *I. typographus*, attacking Norway spruce. The paper presents two studies conducted in the Tatra Mountains in a similar area but using a slightly different methodological approach.

In 1998–2000, the abundance and dynamics of *I. typographus* populations occurring in the 60–80 year old Norway spruce stands were evaluated on 10 sites selected in proximity to the previously established

ozone monitoring sites within the Carpathian range in five countries (Czech Republic, Poland, Slovakia, Ukraine and Romania) (Bytnerowicz et al. 2002). One of the plots was established in the Tatra Mountains in the western part of the Tatra National Park in Poland. Data on several parameters were collected including the captures of adult beetles in pheromone traps, number of attacks, the presence and relative abundance of associated bark beetle species, and the volume of infested trees, reflected in the volume from sanitation felling i.e. the removal of infested trees (Capecki 1981). The volume of such cuts was analysed in the period 1995–2000 and then a yearly average value was calculated in order to estimate stand response to various environmental stresses caused by air pollution (Fig. 1).

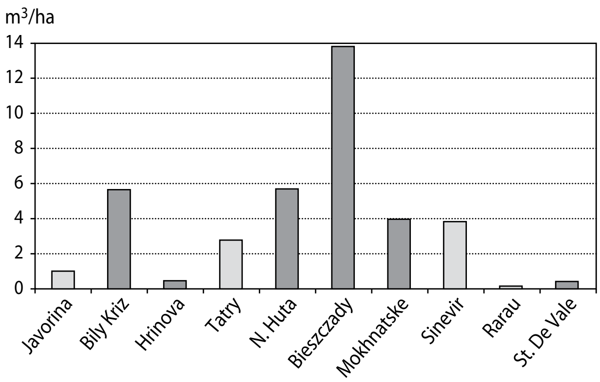

Fig. 1. The volume of infested trees (m³/ha) on sites with low (grey bars) and high (dark bars) ozone concentration in 10 localities in the Carpathians (Javorina, Bílý Kříž – Czech Republic; Tatry, Bieszczady – Poland; Rarau, St. De Vale – Romania; Hriňová, Novoveská Huta – Slovakia, Mokhnatske, Sinevir – Ukraine)

Higher bark beetle population densities were associated with higher ozone levels in stands, while the mean density of insects on infested trees was higher on the plots where ozone levels were lower (Grodzki et al. 2004). This may be attributed to the relatively better health condition of stands where food sources for bark beetles are limited, which results in the infestation of individual trees up to the saturation of available breeding resources. In contrast, stands where ozone levels are higher may provide spatially better food sources, hence the number of trees susceptible to infestation is larger. This results in a higher number of infested trees in a stand but a lower infestation density of individual trees. The relationship is not strong, which suggests that spruce bark beetle dynamics are driven by a complex interaction between the biotic and abiotic factors but not by a single parameter, such as air pollution. Multiple regression analyses in other authors' studies (Nef 1994, Dutilleul et al. 2000) indicate that altitude and soil nutrients, such as nitrogen, phosphorus, and magnesium also have a significant impact on *I. typographus* attack rates. The Carpathian forests vary in their structure, composition, chemistry and biodiversity and, consequently, in their susceptibility to bark beetle attacks. As reported by Økland et al. (2005), the spatial synchrony of *I. typographus* populations decreases significantly beyond the distance of 300 kilometres. This implies that fluctuation cycles over larger areas may be related to significantly different stages of population development, thus comparing their temporal statuses is rather difficult.

The research was continued at a smaller spatial scale in the years 2000–2001 exclusively in the High Tatra Mountains. Three altitudinal transects, consisting of four sites each, were established in 2000 in the High Tatra Mountains on both the Slovak (Tatranské Matliare – Skalnaté Pleso and Vyšné Hágy – Štrbské Pleso, southern slopes) and Polish sides (Poroniec – Włosienica, eastern slopes). Traps containing synthetic pheromones were placed at each site, and ozone concentrations were measured twice each month in close proximity to where bark beetles had been captured. The average ozone concentration value in the entire growing season was used in the correlation analyses because this measure reflected better high mobility of bark beetles. The differences in average captures on the transects were significant and well related with ozone concentrations. The results of this study imply that ozone concentrations may have some effect on bark beetle populations at high elevations. This effect can be characterised as immediate rather than delayed as it is visible already in the same growing season, however the mechanism behind this process is still unknown (Turčáni et al. 2003).

According to Botterweg (1982), *I. typographus* is likely to leave areas where conditions for its reproduction are unfavourable and can spread at distances even larger than 8 kilometres. The mechanism of spreading in habitats with sufficient food sources can be different, thus the spread in the habitats may be more lim-

ited with low bark beetle populations. The distance between the study sites in the Tatra studies varied from 1 to 4 kilometres and the total length of transects varied from 5 to 7 kilometres. Therefore, the movements of individuals might occur between the study sites but not between transects (distances between transects were from 10 to 30 kilometres). If we assume that bark beetles spread in search of suitable habitats, also their captures in pheromones traps should indicate the suitability of stands for *I. typographus*. Thus, it is possible to capture more beetles in more stressed forest stands even if their actual abundance on infested trees is low within a given site.

Air pollution predisposes spruce trees and stands to attacks by certain groups of insects (Grodzki 1995b) both defoliators (Baltensweiler 1985, Schaffelner et al. 1992) and bark beetles, especially *I. typographus* (Christiansen, 1989; Grodzki, 1995a, 1997a). The complex nature of bark beetle – host tree – site interactions seems to contribute to the non-linear relationship between bark beetles and air pollution as found in the Carpathians (Grodzki et al. 2004). Reeve et al. (1995) suggest that the lower level of water stress activates defence mechanisms in trees by stimulating resin production. In manipulated experiments with water stress, the lower frequency of *I. typographus* attacks occurred on trees that were slightly stressed (Turčáni – unpublished data). A similar mechanism might be involved in assessing the effect of ozone concentrations.

In our studies, we used number of beetles captured in pheromone traps to estimate the density of *I. typographus* populations because it was the simplest and most efficient method available. This method was proposed by Bakke (1985) for monitoring bark beetle populations, however, the relationship between beetle captures and population density was poorly recognised. Nevertheless, studies of the relationship between captures and tree infestation indicated that captures might provide an approximate estimate of real *I. typographus* abundance (Turčani et al. 2003, Grodzki 2007).

It was difficult to determine whether ozone concentrations had any effect on forest ecosystems, either positive or negative, as the differences between the concentrations obtained in both studies by Turčani et al. (2003) and Grodzki at al. (2004) were not significant. Schroeder and Eidmann (1986) demonstrated that the direct negative impact of some atmospheric gases was found only when their concentrations were extremely high, however, they studied inert gases and not ozone which is more reactive than O_2, N_2 and CO_2.

A cause-and-effect study is needed to determine the effect of ozone; specifically does it damage host trees by decreasing their resistance, thus making them more suitable for bark beetle attacks (Berryman 1972, Christiansen et al. 1987)? This hypothesis should help us understand or explain the occurrence of bark beetle outbreaks at high elevations where ozone concentrations are usually the highest. However, there is no evidence to support this hypothesis on the basis of our studies. It should be noted that both our studies were conducted in a relatively short period of time, so no data were available throughout the entire outbreak cycle. Nevertheless, a framework was developed and parameters were determined to be used in future studies that that we hope will be continued.

Bark beetle outbreaks – different approach, joint study

Between 1993 and 1998, a massive bark beetle outbreak occurred in the eastern part of the Tatra Mountains. The outbreak was retrospectively analysed by an international team within the research project "TATRY" under the EU 4th Framework Programme. The outbreak-related tree mortality affected Norway spruce stands on both sides of the state border. Because of the different legal regulations governing national parks in Slovakia and Poland, the forest management strategies implemented in the two countries were different (strict nature protection in Poland *vs*. differentiated active forest protection in Slovakia). The course of the bark beetle outbreak was similar in both parts of the studied area – the mean volume of infested trees per hectare, calculated for the entire area, was almost equal in both Polish and Slovak parts (Grodzki et al. 2003, 2006a). However, the degree of mortality and the area of the stands attacked changed more dramatically in the Slovak part, especially in the years 1995–1996 (Fig. 2).

The decade 1990–1999 was characterised by periods of markedly different weather conditions (Fig. 3). It began with extremely variable conditions in 1990 (dry year) and 1991 (wet year); but after 1991, droughts occurred at all altitudes until 1995. Based on the aver-

age temperatures from the Javorina station, the years 1992–1995 can be characterised as dry – warm/cold and the years 1996–1997 as wet – cold (Grodzki et al. 2006a).

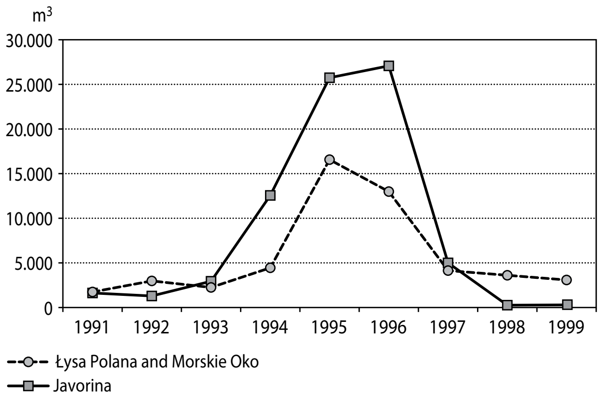

Fig. 2. Volume of trees killed by bark beetles in Polish (TPN – Łysa Polana and Morskie Oko) and Slovak (TANAP – Javorina) part of the outbreak area in the eastern Tatra Mts. in 1991–1999 (cf. Grodzki et al., 2002)

The outbreak started first in Poland, then developed synchronically in both countries (1994–1995) during the period of hot and dry weather in the years 1992–1995 (*cf.* Fig. 2, 3) and collapsed under the cold and wet weather conditions in the years 1996–1997, which were unfavourable for bark beetles but positive for tree resistance. In Poland, most attacks occurred on S and SE slopes despite the fact that east-facing slopes were prevalent. Likewise, proportionally more attacks occurred on western slopes in Slovakia, though NW and SW slopes were most prevalent (Grodzki et al. 2006a). The stands with SE and W exposures generally offer more favourable conditions for bark beetle attacks (Kula 1992, Grodzki 1995a, 2007).

The bark beetle outbreak in the territory of Poland and Slovakia extended over a total area of 4,233 hectares (1,487 and 2,746 hectares, respectively) resulting in the volume of killed/felled trees of 118,924 m^3 (48,534 and 70,390 m^3, respectively) (Fig. 2). The process began in 1994 on several sites that were separated geographically and distributed throughout the study area (Fig. 4a); during the culmination phase (1995–1996) most of the stands in the entire study area were attacked (Fig. 4b), whereas during the retrogradation phase (1997–1999) attacks receded to certain stands close to the state boundary and to the initial outbreak area (Fig. 4c).

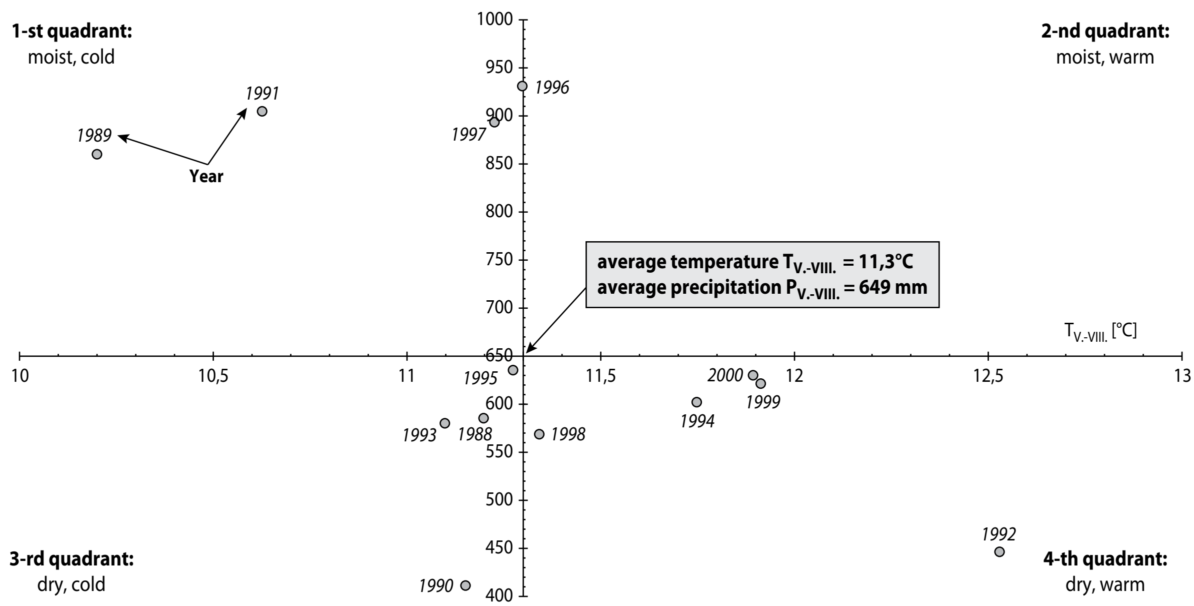

Fig. 3. Average precipitation and temperature data during growing seasons 1988–2000 from two stations in the Tatra Mts.: Javorina (TANAP, Slovakia, 1014 m a.s.l.) and Dolina Pięciu Stawów (TPN, Poland, 1668 m a.s.l.) (Skvarenina unpubl., cf. Grodzki et al., 2006a)

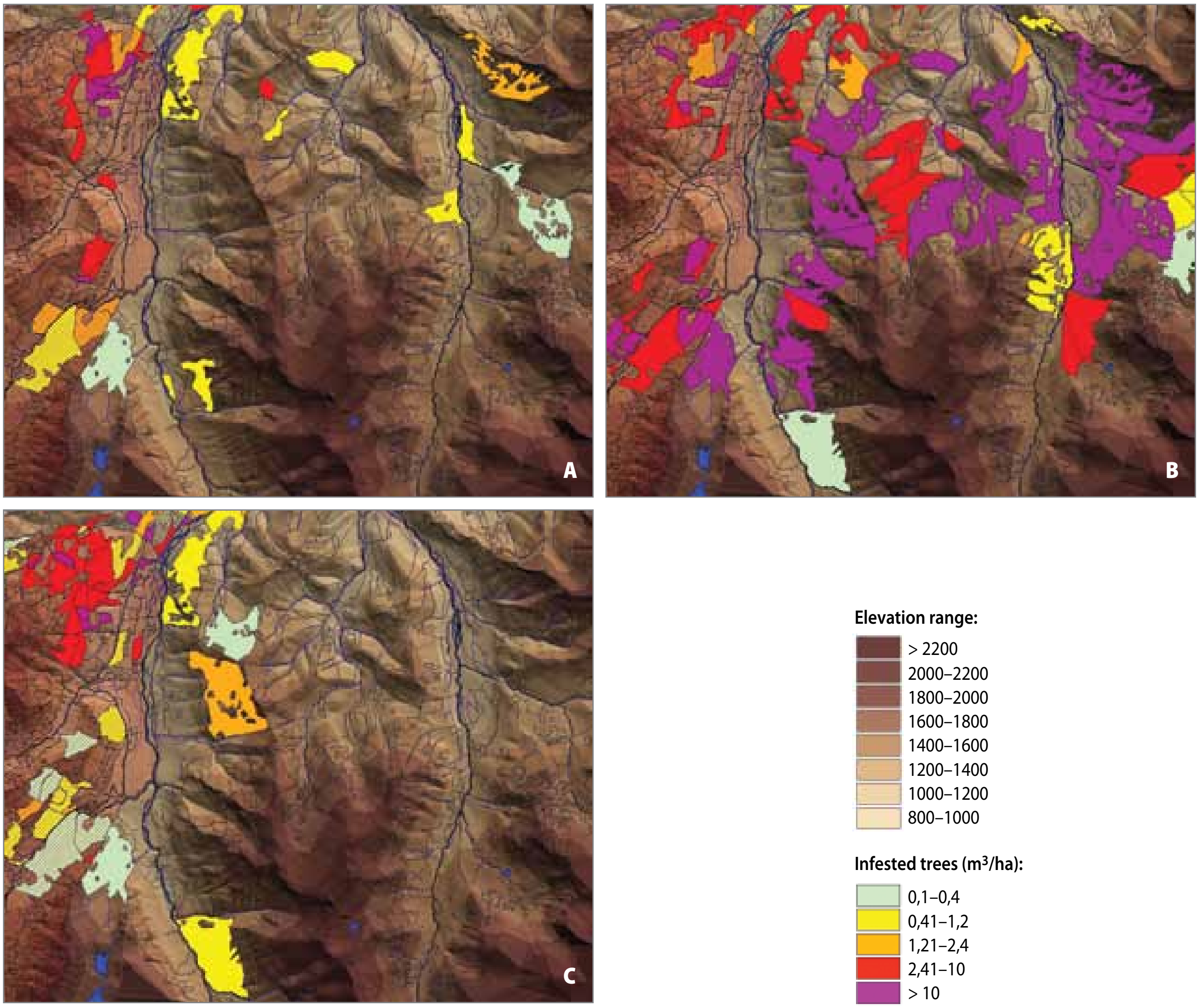

Fig. 4. Spatial development of bark beetle outbreak in the Tatra Mountains in 1991 (A), 1995 (B) and 1999 (C), with the degree of tree mortality (m^3/ha) in individual forest sub-compartments. Passive protection zone in TPN (Poland) marked with red lines

The outbreak, which started in natural spruce stands near the upper timberline in the north facing valleys, but without any prior history of extensive wind damage, may have been caused by the combination of a relatively small and scattered number of wind damage events coupled with a series of hot and dry years. The collapse of the beetle outbreak was probably due to the unfavourable weather conditions in the late 1990s. Such a scenario is known from the large Scandinavian outbreaks (1970–1980) (Worrell 1983, Eidmann 1992), and general pattern in which *I. typographus* outbreaks spread in the Tatra Mountains agrees with the conclusions by other authors (Schwerdtfeger 1955, Stolina 1970, Capecki 1978). During the progradation phase of the outbreak, the spread arises mainly from the new bark beetle spots, while in the culmination and retrogradation phases, the spread is the result of further expansion from the old focal areas. Thus, the dominance of continuous enlargement of spots could be characteristic for *I. typographus* outbreaks and could explain the dominance of the old spots that we observed in later outbreak stages in the Tatra Mountains (Lohberger 1993). A time-dependence of the decrease in the distances between the old and new spots was also recorded: in the first stage of the outbreak, the beetles migrated over fairly long distances and explored available resources, but in later stages, when the availability of weakened trees was more limited, the beetles were more likely to attack only less suitable resources adjacent to

the old spots (Jakuš et al. 2003). The distance between the old bark beetle spots and the newly emerged attacks can range from a few metres, up to two kilometres (Otto and Schreiber 2001, Wichman and Ravn 2001). Genetic investigations on bark beetle sub-populations in the study area indicate that there is a high potential for these insects to disperse (Lakatos 2002). *I. typographus* is capable of dispersing across high mountain ridges (Forsse and Solbreck 1985), thus areas with no pest management could possibly act as a source of bark beetles.

The spatial distribution of attacked stands reflected their age structure, which differed on both sides of the border. In TPN (Poland), total mortality was associated with advanced age (140–245 years) and natural tree mortality, which is normal in old Norway spruce stands. In the Slovak region, the occurrence of high tree mortality in younger stands (100–120 years) may have been associated with human activity, such as intensive sanitation cuttings that were conducted in the attacked stands (Grodzki et al. 2006a).

It was concluded that the spatial pattern of the spread of bark beetle outbreaks is related to the phase of the outbreak, stand characteristics, and the incoming solar radiation of stands on mountain slopes, which results in the insolation of individual bark beetle spots (Netherer and Nopp-Mayr 2005, *cf.* Schopf and Köhler 1995). This increase of solar radiation can result from cutting, felling, or defoliation of neighbouring trees (Jakuš et al. 2003). The two different management approaches may produce two different outcomes – clusters of dead trees in no-management zones, and surviving trees between large clear-cuts in pest management zones. The extent of mortality in the clear-cut zone was, however, proportional to the respective area in the no-management zone (Grodzki et al. 2006a).

In the areas where no control measures were applied, the outbreak collapsed at the same time as in the stands subject to pest control. The main cause of this collapse was probably the effect of cold and rainy weather on trees and bark beetles, as well as an increase in the activity of natural enemies (parasitoids, entomopathogens). This pattern is not easy to elucidate by using statistical methods because bark beetles use ephemeral food sources at the beginning of an outbreak, but the population dynamics is probably influenced by parasitoids, predators and diseases later in the outbreak. However no sufficient data were collected which might confirm the role of this bioregulation complex. Natural enemies were not studied directly, however, their presence was evident in the late stages of the gradation. On the other hand, even if the area of clear-cuts was nearly equal to that of the dead forest area in no-management zones, the utilization of clear-cuts could possibly be lessened by the use of pheromone trap barriers (Jakuš 1998).

Wind damage and bark beetles – impact and management

Situation prior to 2004

The importance of disturbances caused by wind was mentioned in previous chapters, however, in this chapter we explore in greater detail the relationship between wind disturbances and bark beetles. The genesis of the wind problem in the Tatra Mountains can be traced back to the beginning of the 20th century when large areas of pastureland in Slovakia were afforested with spruce monocultures. These stands reached an optimal age at which they become vulnerable to damage from injurious agents in the last decade of the 20th century. The first signs of large-scale disturbances occurred in 2002 when forests (in the area attacked in 2004) suffered an episode of heavy damage by wind (Fig. 5). The wind damaged the trees (mainly spruce) of a volume of 117,000 in Slovakia and 38,700 m^3 (on total area of 3,000 hectares) on the Polish side (Varínsky et al. 2003, Grodzki et al. 2006b). In Poland, most of the fallen and broken trees occurred in the area that was managed under active protection (lower forest-zone spruce stands with an admixture of fir), however, the spruce stands in the area under strict protection were also damaged but to a lesser degree (ca 1,600 m^3). The extent of damage in the late autumn of 2002 was largest since the windthrow events that occurred in 1968 (Bzowski and Dziewolski 1974). In Poland, most damaged trees were processed, however, in Slovakia, a significant volume of damaged spruce timber was not removed from the forests because of their nature conservation status.

The situation in Slovakia was additionally complicated by the fluctuation in the dynamics of bark beetle populations in the entire region. Previous analyses (Turčáni – unpublished data) suggested that peaks in the fluctuations of bark beetle populations occur every 9–10 years. Thus, the years 2002–2003 were the 7th and 8th

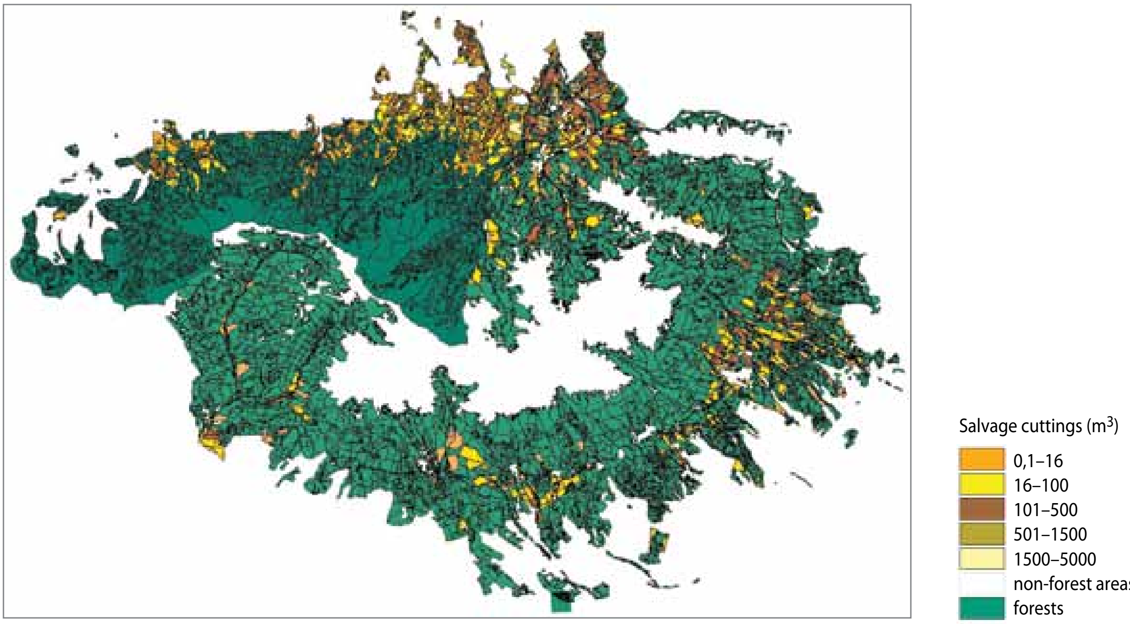

Fig. 5. Spatial distribution of forest stands damaged by wind in the autumn, 2002 in TANAP (Slovakia) and TPN (Poland)

years after the peak years of the previous outbreak in Slovakia. The weather in 2003 was very advantageous for the development of bark beetles and, in combination with the optimal fluctuation phase and optimal food resources in the Tatra Mountains, the infestation of forest stands began to accelerate (Fig. 6, 7). There was about 45 000 m^3 of wood (mainly from wind thrown trees) infested by bark beetles in the area by the end of 2003.

In Poland, during the first growing season after damage (2003), when insects infested the broken and fallen trees left in the forest, the volume of infested standing trees was negligible and the frequency of *I. typographus* was relatively low. In 2004, the area of stands with recognised infestations increased to 1077 hectares and the stands with high bark beetle abundance represented 732 hectares (30.0%), while in 2005, these values increased to 1129 hectares (46.3%) and 876 hectares (35.9%), respectively; this indicates a dramatic increase in the bark beetle population during the second growing season after wind damage (Grodzki et al. 2006b). Wind damage and the abundance of suitable host material were the factors responsible for the bark beetle population increase, whereas insect abundance was enhanced by an extremely long and hot growing season in 2006 when the outbreak entered the epidemic phase (Fig. 6). This outbreak continued to develop in subsequent years, depending on the weather and other environmental conditions.

According to available data, the years 2000–2003 were characterised by warm summers and mild winters with normal precipitation (meteorology station Skalnaté Pleso), while 2004 was colder and wetter than normal; and this might have precipitated a decline in bark beetle abundance. However, long-term analyses conducted earlier (Turčáni – unpublished data) indicated that the weather probably had a lower direct impact on cyclic fluctuations of bark beetles than previously thought, mainly in the progradation phase (2004 is the 9th year of the earlier mentioned short cycle in bark beetle populations, which is typical for the last decades in Slovakia). Thus, the volume of infested trees increased in that year (Fig. 7) and bark beetle attacks occurred over a large area (Fig. 8). The largest concentrations of bark beetles occurred mainly in the eastern regions of the Tatra Mountains (Javorina, Podspády, Tatranská Lomnica and Kežmarské Žľaby in TANAP, Łysa Polana and Zazadnia in TPN). This area in Slovakia (except for Javorina and Podspády) is similar to those heavily damaged by wind on November 19th 2004.

The same temporal pattern was found in two distant wind-damaged forest areas enjoying nature protection status in Poland (Grodzki et al. 2006b), as well as in oth-

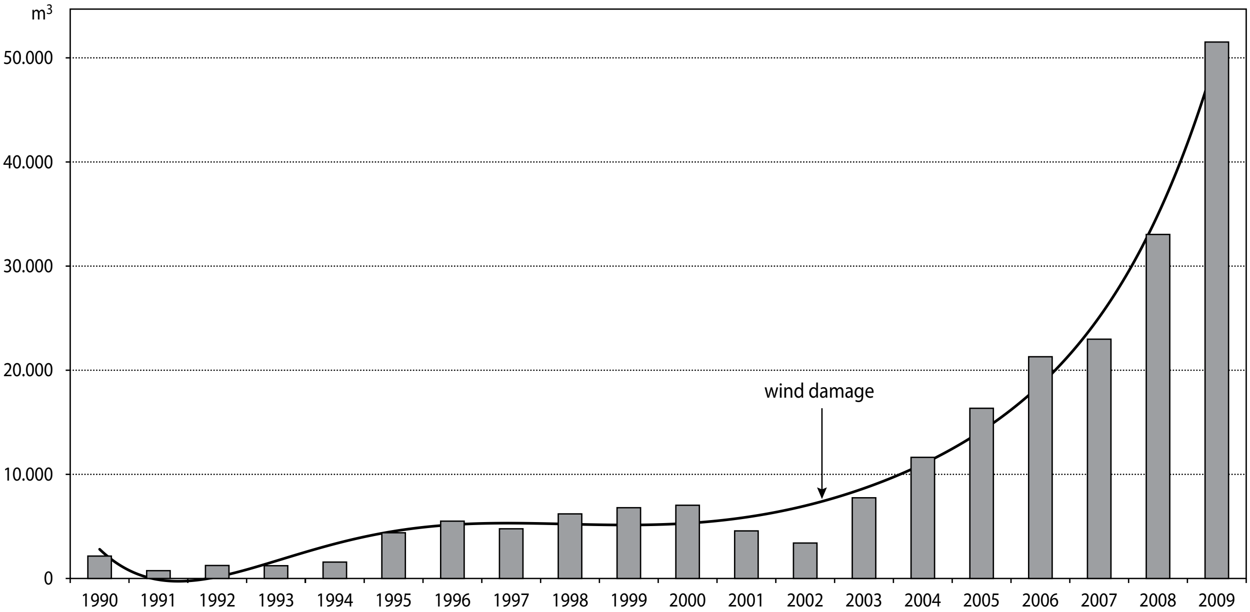

Fig. 6. Volume of trees infested by bark beetles in TPN (Poland) in 1990-2009, prior to and after wind damage (marked by arrow) in 2002

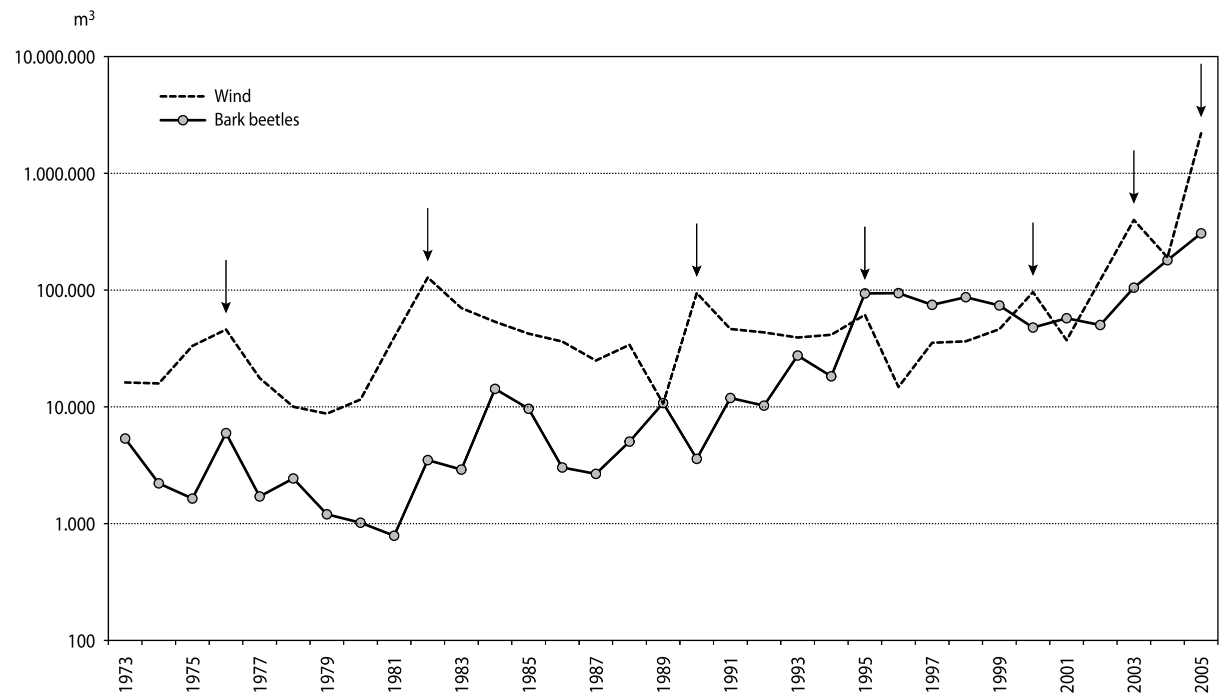

Fig. 7. Tree mortality caused by wind and bark beetles in TANAP (Slovakia) during the period 1973–2005 (arrows represent episodes of intensive wind damage)

er wind-damaged areas in Europe (Forster 1998; Lindelöw and Schroeder 1998, 2001; Göthlin et al. 2000). The increase in *I. typographus* population density is thus most probably related to a temporary improvement of its breeding conditions enhanced by the abundance of fresh logs, and furthered by mechanical damage and

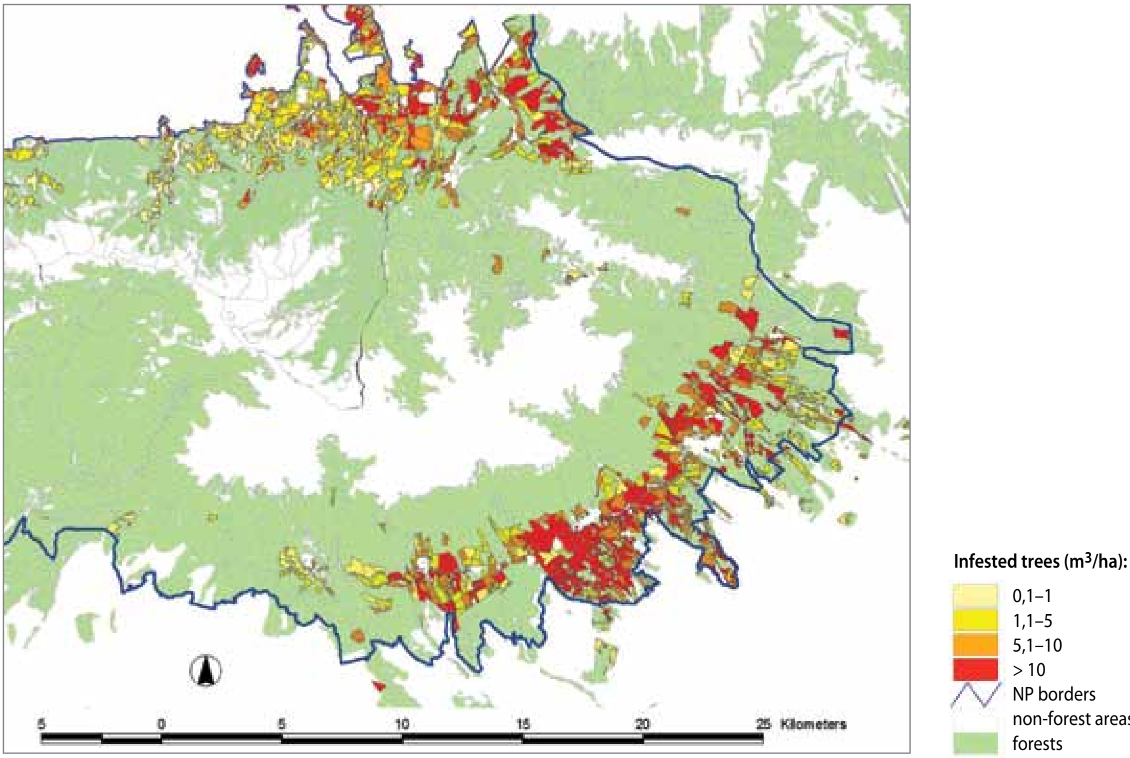

Fig. 8. The volume of salvage cutting due to infestation by bark beetles in TANAP (Slovakia) and TPN (Poland) in 2004

physiological stress in the surrounding fragments of stands that have survived the disaster. The disastrous bark beetle outbreak which started in 2004 continued into 2007, both in the areas embraced by active protection (Fig. 8) where control measures against bark beetle populations were undertaken immediately and in the strict reserves where no intervention was allowed.

Since the early 1990s, windthrow events have become more frequent and the amount of wood infested by bark beetles has significantly increased since the mid 1980s (Fig. 7). The impact of bark beetle attacks in 1982–2003, as well as damage to stands caused by wind action in 1993–2003 may have predisposed the remaining forests to wind which, consequently, destroyed large tracts of forest in November 2004.

Wind disaster in TANAP in November 2004

On November 19th 2004, a catastrophic wind event affected large forest areas in Slovakia including the Tatra region within the TANAP. The wind-damaged stands were located at altitudes between 750 and 1450 m a.s.l., over an area of about 12,000 hectares; the total volume of windthrown and windbroken trees in the territory of the State Forests TANAP was estimated at two million m^3. This was probably the largest wind disaster recorded in Slovakia since 1870 (Kunca and Zúbrik 2006). No catastrophic damage occurred at that time to the adjacent forests in the Polish part of the Tatra Mountains.

Earlier knowledge and experience gained from previous bark beetle outbreaks largely influenced the strategies developed to prevent catastrophic outbreaks in the Tatra Mountains in the future. The evaluation of the situation on a spatial scale began shortly after the disaster occurred in order to obtain additional information essential for more effective management of bark beetle populations. The disturbed forest area was categorised according to the level of threat as a basis for future decision-making.

The majority of the affected forest areas were situated outside the zone enjoying the highest conservation status (nature reserves). Only small forest areas were beyond the territory of the National Park. A decision was made that in the wind-disturbed areas only damaged wood in the National Park but not in nature re-

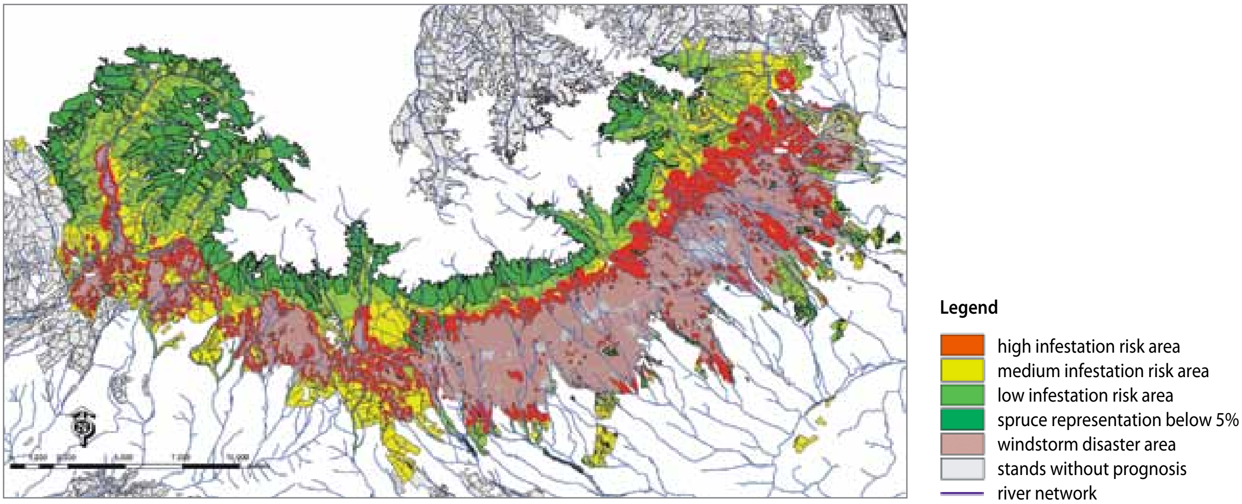

Fig. 9. The assessment of the bark beetle infestation risk in the wind damaged area in TANAP (Slovakia) using the spatial model applied to available parameters

serves would be processed. The question regarding wood processing in the strict nature reserves in TANAP was negotiated between the nature conservation administration and foresters taking into account not only the existing situation but also the strategy for National Park zoning in the future.

The basic rules governing national parks and nature reserves are defined by Slovak law in such a way as to limit the use of control measures. Also earlier information suggested that the likelihood of imminent bark beetle outbreaks was high. It was therefore necessary to categorise the entire affected territory and determine which control measures might be applied in those zones of various conservation status (Zúbrik et al. 2005). For this purpose a bark beetle risk model was needed as an important tool in decision support and planning additional control measures. The first model was developed shortly after the disturbances had occurred and the risk of an outbreak was estimated as extremely high throughout the area. The second model was built in mid 2005 after the necessary data had been collected. The model was based on the following parameters:

– Infestation of bark beetles prior to the windthrow (volume of infested trees cut in salvage felling);
– Selected stand and environmental parameters;
– Data from two long-term bark beetle survey transects (Turčáni et al. 2003);
– Available information about bark beetle spread potential.

Bark beetle risk assessment expressed as a mathematical model was then entered into the GIS environment as a spatial application (Fig. 9). The risk of an outbreak was much lower in the western part of the wind-damaged area, however, the model predicted a high risk of bark beetle attacks on the remaining trees also in the eastern region. In forest areas with a lower conservation status, 91 per cent of the total volume of damaged wood was processed in 2005; only 125,000 m^3 of wood was retained to be removed in 2006. The area with the highest conservation status is divided into two zones – nature reserves which will hold the highest status and those which will probably lose their status. Due to this new zoning, 28 per cent of damaged wood was not processed. In 2005, the populations of bark beetles – mainly *I. typographus* – were generally at a low level. The first swarm attacked mostly damaged trees, so the infestation was very low and spatially heterogeneous (*cf.* Grodzki et al. 2006b). However in 2005, a high infestation of stands occurred in some areas characterised by a chronic forest decline and persistently high populations of bark beetles. The outbreak developed synchronically in undamaged stands on the Polish side of the Tatra Mountains (Fig. 6).

There are two approaches (passive nature conservation *vs.* active forest protection) that differ in the perception of the role of bark beetle outbreaks. Foresters see bark beetles as pests damaging valuable forest resources, while nature conservationists view such

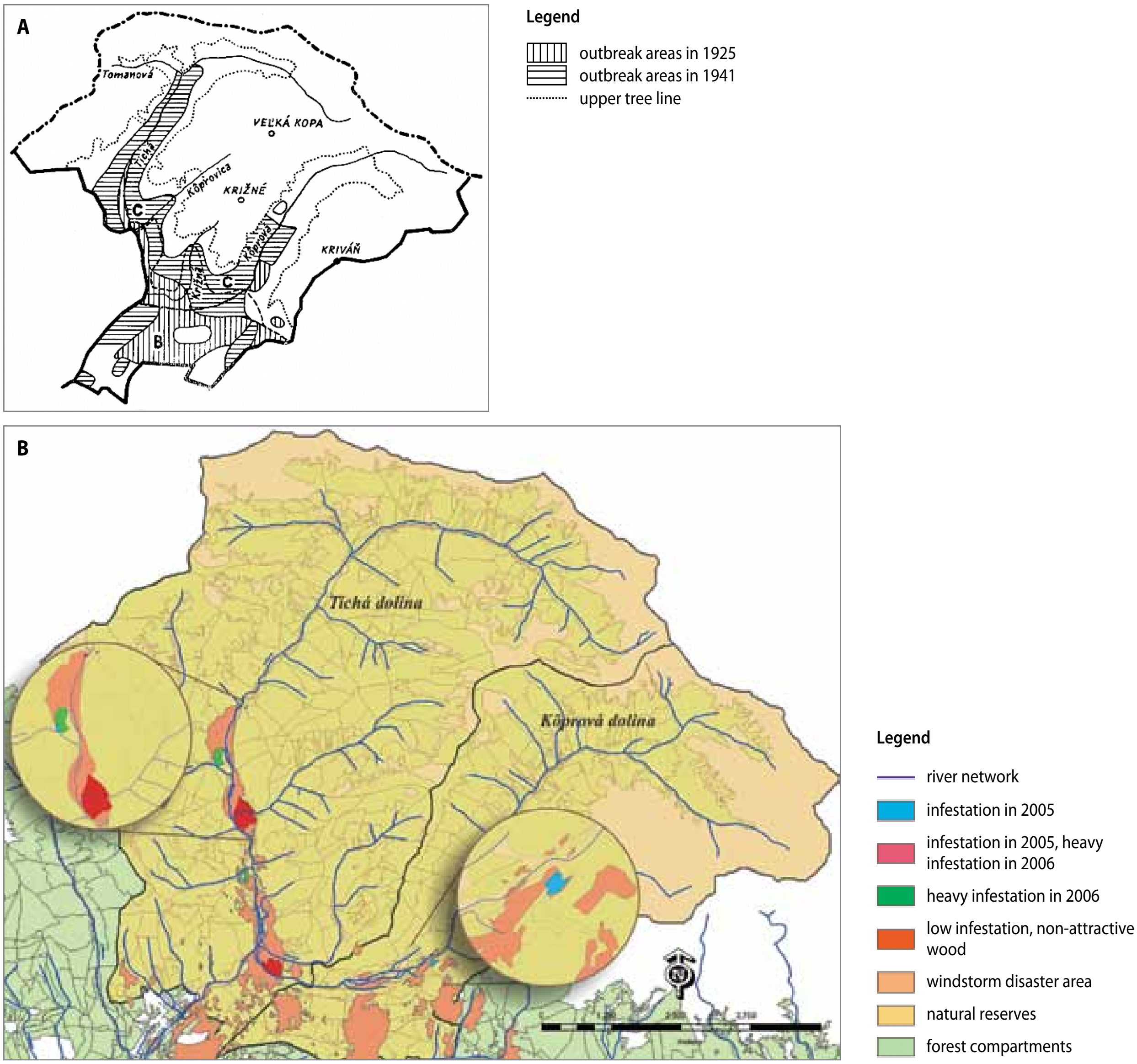

Fig. 10. Historical data on bark beetle outbreak areas in the Tichá and Koprová valley (TANAP, Slovakia) according to historical records (Zúbrik et al 2006) (A) and the results of intensive survey of bark beetles populations conducted in the autumn 2005 and 2006 (B)

outbreaks as a natural component of mature stands. Problems are most severe in those areas where outbreaks occurred repeatedly in the past, and which were not classified into the highest conservation category. The Tichá and Kôprová valleys can serve as an example of this controversy. Both valleys suffered one of the largest bark beetle outbreaks in the territory of the Tatra Mountains (Zúbrik et al. 2006), probably as a consequence of the damaging impact of winds and fires that had occurred in these regions in the past (Fig. 10A).

In order to obtain more precise data, an extensive survey of the area was conducted. The results indicate that the spatial structure of the infestation was extremely heterogeneous in late 2005. Trunks were infested mainly in close proximity to the pheromone traps up to a distance of 10 to 20 m. Moderately to heavily infested trunks were also found adjacent to the traps (Fig. 10B).

These sites were usually located in the vicinity of known bark beetle sites from the past years (Hlinský Hrebeň ridge). The infestation was often observed on the south-facing terrain ribs and talus cones. However, even at these sites, the majority of trunks did not show any signs of infestation.

2006 saw a rapid increase in bark beetle abundance on residual trees, similar to the temporal pattern described after the wind damage in 2002. Then the probability of bark beetle outbreaks in the Tichá and Kôprová valleys became very high.

Geostatistical methods were used to develop a map of spatial distribution of *I. typographus.* A negative correlation of its occurrence with elevation gradient was assumed to be a starting point for the modelling. This "exercise" reflects the state of our knowledge that fewer numbers of beetles are trapped at higher elevations which is attributed to lower temperatures as a limiting factor. This gradient is very well defined in the region of the Tatra Mountains (Turčáni et al. 2003). The resultant map clearly shows that after reaching a certain elevation (approximately 1200–1300 m a.s.l.) the environmental conditions for bark beetles became unfavourable and that in 2005 the potential of this environment to support their survival approached zero. The map also shows the focal areas where the highest numbers of individuals were captured.

The fundamental control measures undertaken in 2006 consisted mainly in pheromone mass trapping first of all in areas with a higher conservation status. Additional control measures were applied in areas with the lowest conservation status and consisted in the use of trap trees (prepared from broken trees), pheromone baiting of damaged trees and logging residues, as well as identification and removal of infested standing trees.

Conclusions

– Tree mortality caused by bark beetles in the Tatra Mountains is one of the most vital factors influencing the development of near-natural and artificially established spruce forests. The results suggest that most susceptible to periodic bark beetle outbreaks are mainly secondary (planted) spruce forests in the lower elevation zone.
– Bark beetle populations are driven by natural abiotic and biotic yet not-well recognised factors which affect their population dynamics. Additional research on the bark beetle – spruce forest interaction should be a high priority.
– Ephemeral situations like natural disturbances (mainly – wind damage) are crucial for the expansion of bark beetle populations; subsequent weather conditions may contribute to epidemic situations.
– The results indicate that the effect of air pollution on bark beetle populations is indirect and complex and that disturbances in tree physiology and natural resistance may be of key importance for the bark beetle population dynamics.
– An active forest protection approach is badly needed in the secondary Norway spruce stands affected by human activity in the past. To prevent serious problems in the secondary and also near-natural spruce forests in the future, the percentage of spruce in such stands should be reduced. This recommendation does not concern forest areas under strict (passive) nature protection.
– Bark beetle populations in natural and near-natural stands (mainly in the upper montane zone – without an influx of individuals from artificial stands) are regulated by natural mechanisms; bark beetles are therefore a natural factor contributing to forest development, including the transition of future spruce generations.

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